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ABSTRACT

Plant growth is influenced by above- and belowground environmental conditions and increasing atmospheric carbon dioxide (CO_2) concentrations enhances growth and yield of most agricultural crops. This review covers current knowledge on the impact of increasing CO_2 concentration on root dynamics of plants in terms of growth, root/shoot (R/S) ratio, root biomass, root length, root longevity, root mortality, root distribution, root branching, root quality, and the response of these root parameters to management practices including soil water and nutrients. The effects of CO_2 concentration on R/S ratio are contradictory due to complexity in accurate underground biomass estimation under diverse crops and conditions. Roots become more numerous, longer, thicker, and faster growing in crops exposed to high CO_2 with increased root length in many plant species. Branching and extension of roots under elevated CO_2 may lead to altered root architecture and ability of roots to acquire water and nutrients from the soil profile with exploration of the soil volume. Root turnover is important to the global C budget as well as to nutrient cycling in ecosystems and individual plants. Agricultural management practices have a greater impact on root growth than rising atmospheric CO_2 since management practices influence soil physical, chemical, and biological properties of soil, consequently affects root growth dynamics in the belowground. Less understood are the interactive effects of elevated CO_2 and management practices including drought on root dynamics, fine-root production, and water-nutrient use efficiency, and the contribution of these processes to plant growth in water and nutrients limited environments.

Global climate change has emerged as an important environmental challenge due to its potential impact on biological systems on Earth. Atmospheric concentrations of CO_2 have steadily increased from approximately 315 μmol mol^{-1} in 1959 to a current atmospheric concentration of approximately 385 μmol mol^{-1} which converts to an average annual increase rate of nearly 2 μmol mol^{-1} (Keeling and Whorf, 2005). At this rate of increase, concentrations are projected to reach levels between 500 and 1000 μmol mol^{-1} by 2100 (IPCC, 2007). Carbon dioxide is not only a major greenhouse gas, but essential to plant growth (Kramer, 1981; Dahlman et al., 1985; Warrick, 1988; Kimball, 2011). The flow of C from photosynthesizing tissues of higher plants, through the roots and into the soil is one of the key processes in terrestrial ecosystems. Increases in atmospheric CO_2 concentration will have direct and indirect effects on crop plants and increases in CO_2 will generally increase plant productivity and water-use efficiency (Drake and Gonzàlez-Meier, 1997; IPCC, 2007). The long-term response to CO_2 remains uncertain and will depend on environmental constraints. Yields of most agricultural crops will increase under elevated CO_2 with productivity increases in the range 15 to 41% for C_3 crops and 5 to 10% for C_4 crops (Cure, 1985; Kimball, 1983; IPCC, 2007; Lotze-Campen and Schellnhuber, 2009).

Analyses of plant responses to elevated atmospheric CO_2 have focused largely on aboveground processes; however, understanding the effects on photosynthesis are insufficient to answer questions about overall plant response to a changing atmosphere. A whole-plant perspective is required to understand the critical feedbacks and adjustments occurring within a plant and between plants and soil. An overlooked and under studied aspect of plant response to rising CO_2 is on belowground processes. The vital role of roots as an interface between the lithosphere and biosphere is necessary to understand plant response to elevated CO_2. Despite the important role roots play, they have been an understudied component of agricultural research since they exist underground. Root health in crop plants will play a major role in providing sustainable highly productive crops with the ability to cope with climate changes; however, the effect of increasing CO_2 on root growth and development is poorly understood. Climate change is expected to increase the incidence of extreme weather events, such as drought, heat waves, and heavy precipitation and floods, causing crop production to become more variable (IPCC, 2001, 2007; Hatfield et al., 2011). Under these conditions, many of the environmental factors, for example, water, temperature, light, nutrition, salinity, air pollutants, and competition have significant interactions with CO_2 concentration on root responses for numerous species as summarized by Rogers et al. (1994). Understanding of dynamics of crop roots is important from the point of view of management of available resources to increase the productivity of crops and resilience of crops to climate stress.

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Abbreviations: ABA, abscisic acid; FACE, free air carbon dioxide enrichment; R/S, root/shoot ratio.

The objectives of this review are to express the importance of understanding the dynamic of crop species and to summarize the current knowledge on the effect of increasing CO_2 concentration on root growth, R/S ratio, root biomass, root length, root longevity, root mortality, root distribution, root branching, root quality, and the response of these root parameters to soil management practices, and interactions with soil water and nutrient status.

Root Biomass

Increasing atmospheric CO_2 significantly increased the final plant biomass, aboveground biomass, leaf area and belowground biomass (Obrist and Arnone, 2003). Increased root growth contributes to root biomass and root dry weight under elevated atmospheric CO_2 regardless of species or study conditions (Rogers et al., 1994, 1996). Roots often exhibit the greatest relative dry weight gain among plant organs (Imai and Murata, 1976; Wittwer, 1978; Rogers et al., 1983; Imai et al., 1985; Hocking and Meyer, 1991; Norby et al., 1992), even more than aboveground biomass or leaf area production (Norby, 1994; Rogers et al., 1999; Pritchard and Rogers, 2000; Bernacchi et al., 2000). However, increased allocation of C to plant-root systems in response to CO_2 levels may offset losses from increased activity of soil microorganisms (Suter et al., 2002). Increases in root mass may benefit mycorrhizal fungi and production of glomalin, a glycoprotein produced by endomycorrhizae contributing to soil aggregation (Rillig et al., 1999).

Wheat (*Triticum aestivum* L.) (Chaudhuri et al., 1990; McMaster et al., 1999, Wechsung et al., 1995), sorghum [*Sorghum bicolor* (L.) Moench](Chaudhuri et al., 1986), Black gram (*Vigna mungo* var. *mungo*; Vanaja et al., 2007), and soybean [*Glycine max* (L.) Merr.] (Del Castillo et al., 1989; Rogers et al., 1992), have shown increases in root dry weight under CO_2 enrichment (Rogers et al., 1994). Laboratory studies on cotton (*Gossypium hirsutum* L.) plants in a free air carbon dioxide enrichment (FACE) project revealed dry weights, lengths, and volumes of taproots, lateral roots, and fine roots were higher for CO_2–enriched cotton plants with a short-term exposure to increased CO_2 for 6 wk (Prior, 1992; Prior et al., 1994a, 1994b; Rogers et al., 1993). Observations from a spring wheat FACE study revealed a 37% increase in total root dry mass in the CO_2–enriched plot during early vegetative growth (stem elongation) and sustained root growth rates until anthesis (Wechsung et al., 1999). The combined effect of temperature and elevated CO_2 concentration affect growth and development of roots, Pilumwong et al. (2007) observed in groundnut (*Arachis hypogaea* L.) that fibrous root dry weight increased with increased CO_2 when plants were grown at 25/15°C, but decreased with increasing CO_2 at 35/25°C. At 35/25°C, there was greater root dry weight by 34% at 400, 14% at 600, and 7% at 800 μmol mol^{-1} compared with 25/15°C.

Narrow leaf plantain (*Plantago lanceolata*) seedlings grown under elevated CO_2 (800 μmol mol^{-1}) produced 180% greater root dry matter than at 400 μmol mol^{-1} and amount of plant C recovered was 3.2 times greater from the elevated CO_2 treatment (Hodge and Millard,1998). The same response was found for raspberry (*Rubus idaeus* L.) plantlets (Laforge et al., 1991). A meta-analysis of the effects of elevated CO_2 on woody plant species (Curtis and Wang, 1998) found biomass responses were strongly affected by environmental stress factors and to a lesser degree by duration of CO_2 exposure. They reported belowground biomass responses to CO_2 were highly significant overall (+38%, k = 64) but were affected by stress and length of exposure to increased CO_2. About 36 studies reported underground biomass under unstressed trees increased by 41.5% under elevated CO_2. Some plant species namely, kidney vetch (*Anthyllis vulneraria*), hoary plantain (*Plantago media*) (Ferris and Taylor, 1993), spartina with shallow rooting depth (Curtis et al., 1990), and common bean (*Phaseolus vulgaris* L.) (Salsman et al., 1999) exhibited no response of root dry matter production to elevated CO_2.

Root growth of crop plants is often stimulated to a greater extent than other plant parts to increased CO_2 concentration (Rogers et al., 1994; Norby et al., 1992; Kimball et al., 2002; Pritchard and Amthor, 2005; Heinemann et al., 2006; Vanaja et al., 2007). Hodge and Millard (1998) observed belowground growth was stimulated in narrow leaf plantain seedlings with increased CO_2 concentration than aboveground components. In maize (*Zea mays* L.) grown under elevated CO_2 relative growth rate of maize roots was increased compared to the relative shoot growth rate (Whipps, 1985) because of increased C translocation to the roots. Pilumwong et al. (2007) reported increased root growth of groundnut due to increasing CO_2 concentration. With no limitations to water and nutrients, elevated CO_2 increased root and shoot growth of most plant species including tree species (Obrist and Arnone, 2003; Rogers et al., 1996; Pregitzer et al.,1995) but the response varied among species (Hanley et al., 2004). Salsman et al. (1999) found increased CO_2 affected root and shoot growth of *Phaseolus acutifolius* but not *P. vulgaris* due to increased concentration of starch in roots of *P. acutifolius* by 10-fold, while root concentrations of abscisic acid (ABA) doubled and caused more C to be allocated to root growth. Several laboratory studies have reported that roots have the capacity to produce significant amounts of ABA (Walton et al., 1976; Cornish and Zeevaart, 1985; Zhang and Davies, 1987) but applications of ABA have been shown to both increase (Mulkey et al., 1983; Pilet and Saugy, 1987) and decrease root growth (Watts et al., 1981; Jones et al., 1987).

Growth and morphology of four native chalk grassland herbs roots responded differently to increasing CO_2 (Ferris and Taylor, 1993). Root growth and biomass was stimulated by elevated CO_2 for *Sanguisorba minor* and *Lotus corniculatus* with no significant effect on growth and root biomass for *A. vulneraria* or *P. media*. They suggested these growth and root responses could potentially lead to changes in the structure of this plant community with continued increases in CO_2. Increasing CO_2 in greenhouse environments increased the percentage of cuttings which formed roots in a range of ornamental and floricultural species (Lin and Molnar, 1981; French and Alsbury, 1989), including raspberry plantlets (Laforge et al., 1991).

Agricultural management practices may have a greater impact on root growth and soil C storage than rising atmospheric CO_2 (Canadell et al., 1996b; Paustian et al., 1996) because tillage systems influence soil temperature (Dwyer et al., 1995), mechanical resistance (Cox et al., 1990), macropore continuity (Roseberg and McCoy, 1992), and available soil water (Cox et al., 1990) through the effects on rooting depth and root distribution with depth. Rooting depth varies with

season, soil texture, and tillage, and increased rooting depth is associated with increased tillage and decreased soil moisture in surface soil layers (Dwyer et al., 1996). Soil water content in the upper soil layers is confounded by reduced soil water holding capacity and thus plant growth and root development depends on rainfall distribution (Lampurlanés et al., 2001).

At the present time, the interactions of CO_2 enrichment and agricultural management practices on plant root growth are not well understood (Swinnen et al., 1995; van Noordwijk et al., 1994). Although a substantial quantity of data indicates that root spatial distributions are significantly affected by tillage practices, it remains unclear whether temporal or spatial distribution of roots differs among conventional compared with conservation tillage systems. Swinnen et al. (1995) found that decay and turnover in barley (*Hordeum vulgare* L.) roots were higher in conventional agricultural systems than in a production system characterized by reductions in nutrient input, soil tillage, and use of biocides, but were not different in wheat under the same management scenarios. In another study, sugar beet (*Beta vulgaris* L.) grown with minimum tillage had lower fine-root production than in the conventional cropping system, whereas fine-root production of wheat was unchanged (van Noordwijk et al., 1994).

Prior et al. (2005) studied the effects of management and CO_2 on aboveground biomass production with an emphasis on changes in soil C storage. They found a substantial increase in soil C concentration at the 0- to 5-cm depth increment in the conservation system compared to the conventional system, and in the CO_2–enriched compared to ambient plots, after two cropping cycles (4 yr). Pritchard et al. (2006) concluded that CO_2 enrichment enhanced cumulative seasonal root length production (+58%) and mortality (+59%) in conventionally managed sorghum, but had no effect in plots with conservation systems. Sorghum under CO_2 enrichment produced more roots at shallow soil depths compared to ambient plots and this additional root production occurred early in the growing season. Conventionally managed sorghum produced less root length in the top few centimeters of soil compared to conservation plots due to increased soil water availability in the conservation tillage plots. Seasonal root length mortality and production were higher at the shallower soil depths in the conservation plots than in the conventional plots. Increases in root mortality in CO_2–enriched plots were proportional to production increases and no effect on root longevity which associated with depth in the soil profile (Pritchard et al., 2006). This was probably caused by the effects of tillage on soil water content due the presence of surface residues coupled with no-till management enhance soil moisture absorption and retention compared to conventional tillage with no residue (Newell and Wilhelm, 1987).

A particular limitation to understanding root dynamics is that most studies do not include measurements below a meter (Nepstad et al., 1994; Batjes, 1996; Canadell et al., 1996b; Jobbagy and Jackson, 2000; Guo and Gifford, 2002; Schenk and Jackson, 2002a, 2002b; Robinson, 2004; Bradley et al., 2005; Lorenz and Lal, 2005; Mokany et al., 2006; Qin and Huang, 2010; Wang et al., 2010). Baker et al. (2007) argued depth of root sampling confounded understanding the impact of tillage and management factors on root growth, root turnover, distribution, etc. and sequestration of C at different depths in the soil.

Roots of drought-stressed plants grown with elevated CO_2 produced significantly higher root dry mass than roots of well-watered plants grown with ambient CO_2 (Chaudhuri et al., 1990). These responses in root growth and morphology led to elevated CO_2 and reduced soil water supports the hypothesis that plants grown in a high CO_2 environment may better compensate to soil-water-stress conditions (Wechsung et al., 1999; Schenk and Jackson, 2002b). An adoption mechanism of plants to water stress condition occurs by physiological and biochemical changes in the plant. Eggplant *(Solanum melongena* L.) roots showed low hydraulic conductance at repetitive stress due to synthesis and accumulation of suberin in the root cells under elevated CO_2 and this change in root structure may occur from synthesizing suberin lipids in endo- and exo-dermis layers regardless of soil water availability or stress intensity. Lowering conductance is highly desirable for agricultural plants when water supply is limited in the growth and development stage (Sarker and Hara, 2009). These observations suggest increasing CO_2 concentration in the global atmosphere might be beneficial for using soil water by minimizing transpiration loss and lowering hydraulic conductance under higher CO_2. In a comprehensive review of FACE experiments on agricultural crops, Kimball (2011) and Kimball et al. (2002) determined that for a 300 μmol mol^{-1} increase in atmospheric CO_2 concentration, the root biomass of wheat, ryegrass (*Lolium multiflorum* Lam.), and rice (*Oryza sativa* L.) increased 70% with ample water and N, 58% at low N, and 34% at low water, while clover experienced a 38% increase at ample water and N, plus a 32% increase at low N. The changes were greatest in cotton with a 96% increase in root biomass at ample water and N. Another FACE study on cotton and sorghum in monoculture and two plant densities under dry and wet soil water condition was conducted by Derner et al. (2003) and showed total root biomass in the upper 1.2 m of the soil was not influenced by CO_2 or soil moisture in monoculture or in mixture; however, under dry conditions there were significantly more roots at soil depths below 45 cm. Sorghum roots comprised 81 to 85% of the total roots in the low density mixture and 58 to 73% in the high density mixture. Carbon dioxide enrichment partly offsets the negative effects of interspecific competition on cotton in both low and high density mixture by increasing aboveground biomass (Derner et al., 2003). The interacting effects of CO_2 and watering frequency on wheat root growth and nutrient uptake pattern increased water use per plant 1 to 25 times at 350 than at 700 μmol mol^{-1} CO_2 and 1 to 4 times in the "wet" compared to the "dry" treatment (Van Vuuren et al., 1997). Root biomass increased with CO_2 and with watering frequency. Nutrient uptake was affected and there were interactions with water availability but interactions were different for N, K, and P, due to differences in nutrient availability and mobility in the soil (Van Vuuren et al., 1997).

Root growth is positively affected by increases in CO_2 concentration across almost all species and is often stimulated more than shoot biomass. There is no simple assessment of the interacting effects of soil physical conditions and nutrient availability and the interaction with increasing CO_2 on root and shoot growth. A summary of the combined effects of increased CO_2 for the different root parameters is shown in Table 1.

Table 1. Overall effects of increased CO_2 on various root parameters.

Root parameter	Species	Type of CO_2 enrichment	Overall effect
Root biomass/ growth	Agricultural plants, groundnut, grassland herbs	Laboratory studies, greenhouse studies	Increase in root growth was larger than shoot growth and root biomass increased as part of overall growth response to increased CO_2.
Root/shoot (R/S) ratio	Agricultural plants, groundnut, grassland herbs, forest species	Laboratory, greenhouse, controlled chamber studies	Results vary among studies; however, 60% of studies show a positive response on R/S, 37% show a negative response, and 3% show no response (Rogers et al., 1996). Under limited soil water or nutrient availability, responses to increased CO_2 are more variable.
Root length/ rooting depth	Agricultural plants, groundnut, grassland herbs, forest species	Laboratory, greenhouse, controlled chamber studies	Increased root length across species is the most common response observed. Root branching also increased with CO_2 enrichment (Rogers et al., 1994).
Root branching	Agricultural plants, groundnut, grassland herbs, horticultural species	Laboratory, greenhouse, controlled chamber studies, free air carbon dioxide enrichment (FACE) studies	Increased root branching is commonly observed in most species and more evident in the upper soil profile.
Root thickness, quality, diameter	Agricultural plants, groundnut, grassland herbs, horticultural species, forests	Laboratory, greenhouse, controlled chamber studies	Increased root thickness and diameter are most commonly observed. Diameter changes are more difficult to quantify.
Root mortality/ root turnover	Agricultural plants, groundnut, grassland herbs, horticultural species, forests	Laboratory, greenhouse, controlled chamber studies, FACE studies	Increases in root mortality and turnover rates are observed across species with increased CO_2. There is an interaction with temperature, soil moisture, and nutrient supply which confounds observations on root turnover rates.

Root/Shoot Ratio

Exposure of plant canopies to high CO_2 concentration often stimulates growth of shoots and roots, but the question remains whether elevated atmospheric CO_2 concentration affects root and shoot growth proportionally (Rogers et al., 1996). The general consensus is that photosynthesis and C allocation to plant roots increases as atmospheric CO_2 rises which leads to an increase in above and below biomass (Del Castillo et al., 1989; Norby et al., 1992; Rogers et al., 1994). Root/shoot ratio is the simple calculation of the ratio of root dry mass to shoot (or stem) dry mass and should serve as a measure of the preferential allocation of C to roots or shoots. Allen et al. (1988) reported that soybean grown under increased CO_2 maintained a similar partitioning of C into their respective components. Similar results were reported by Baxter et al. (1994) in grasses, but roots often exhibit the greatest relative dry weight gain under high CO_2 (Hocking and Meyer,1991; Imai and Murata,1976; Imai et al., 1985; Norby et al.,1992; Rogers et al.,1983). The partitioning pattern of photosynthates depends on plant development stage, plant species, and plant growth conditions along with physiological factors (Van Veen et al., 1991). Various studies have shown between 10 and 40% of the total net C assimilation of crops was transferred to underground biomass in the form of roots, microbial and soil biomass, and respired CO_2 and organic compounds (Barber and Martin, 1976; Whipps, 1984; Helal and Sauerbeck, 1986; Liljeroth et al., 1990; Keith et al.,1986).

Observations on R/S response to CO_2 are contradictory as evidenced by the wide range of results obtained from different studies. Oechel and Strain (1985) found root growth under increasing atmospheric CO_2, plants allocated proportionately more C belowground, increasing R/S ratios. The range of response in R/S among crop plants to CO_2 doubling ranged from a 8.5% decrease to a 6.4% increase, except in sweet potato [*Ipomoea batatas* (L.) Lam. var. batatas], in which a 34.9% increase was observed (Cure, 1985). Results showed R/S was not significantly affected by higher CO_2 concentration in *Larrea tridentate*, a desert herb (Obrist and Arnone, 2003), tall grasses (Mo et al., 1992), four native chalk grassland herbs (Ferris and Taylor, 1993), and winter wheat (Chaudhuri et al.,1990; Havelka et al., 1984). Many studies showed increased R/S (Rogers et al., 1983; Biswas and Hileman, 1985; Idso et al., 1988; Baker et al., 1990; Rogers et al., 1992; Ceulemans and Mousseau, 1994; Pritchard et al., 1999; Rogers et al., 1999), while other studies showed decreased R/S (Salsman et al.,1999; McMaster et al., 1999). In field studies, an increase in the proportion of total dry mass in tubers after exposure to increased CO_2 was observed for sweet potato (Biswas and Hileman, 1985; Bhattacharya et al., 1990), carrot (*Daucus carota* L.), and radish (*Raphanus sativus* L.) (Idso et al., 1988). Idso et al. (1988) suggested that plants whose primary yield component is produced aboveground, atmospheric CO_2 enrichment has a significant effect on R/S. Increases in R/S occurred more frequently for agronomic crops, particularly root and tuber crops and natural community species. Substantial CO_2 research conducted with several forest tree species namely, shortleaf pine (*Pinus echinata* Mill.) (Norby et al., 1987; O'Neill et al., 1987b), virginia pine (*P. virginiana* Mill.) (Luxmoore et al., 1986), white oak (*Quercus alba* L.)(Norby et al. (1986a, 1986b; O'Neill et al., 1987b; Norby and O'Neill, 1989), yellow poplar (*Liriodendron tulipifera* L.) (O'Neill et al., 1987a; Norby et al., 1992), and N-fixing woody plants (Norby, 1987) have revealed an increased R/S, C allocation to roots, root exudation, nutrient uptake, and mycorrhizal colonization under elevated CO_2.

Rogers et al. (1996) summarized a substantial variation in R/S response in crop plants across a range of experimental conditions. He reported crops showed positive responses in R/S to elevated CO_2, 59.5% of 264 observations from 62 reports; negative responses appeared 37.5% of the studies and 3.0% of the studies showed no response (Table 1). There is no general consensus among researchers on the degree of positive response on R/S of

different species; however, these results are tempered by the interactions with water and nutrient management in the soil profile.

Under non-limiting conditions of water and nutrients for growth, dry matter partitioning to the root is moderately changed by CO_2 enrichment. However, increases in R/S, frequently observed under limiting conditions of water and/or nutrients, allows the plant to explore a greater soil volume and extract more water and nutrients (Stulen and den Hertog, 1993). Bazzaz (1990) stated that there would be an increase in C allocation to roots when nutrients and water were limiting. Biomass allocation models such as functional balance developed by Davidson (1969) and C/nutrient substrate ratio developed by Reynolds and Thornley (1982) predicted increases in tissue C/N ratios as N becomes more limiting relative to C leading to increased biomass allocation to roots. Eamus and Jarvis (1989) summarized that under low nutrient conditions there would be an increase in R/S, and this conclusion was confirmed by Ceulemans and Mousseau (1994). There are confounding effects of increasing CO_2 on root allocation and developmental rate and Norby (1994) observed a small (+6%) increase in R/S at high CO_2, with no significant response under nutrient stress. McGuire et al. (1995) and Wullschleger et al. (1995) did not find a significant CO_2 effect on biomass allocation between roots and shoots. The interactions between nutrient status and CO_2 are not clearly defined because the conclusions by Norby et al. (1987) were that limiting nutrients may promote partitioning to the roots and assimilate partitioning under high CO_2 may depend on nutrient status (Lawlor and Mitchell, 1991) and requires that we quantify the nutrient levels in the soil when interpreting R/S responses.

The direct effect of increasing CO_2 on R/S has no clearly defined conclusion (Stulen and den Hertog, 1993; Rogers et al.,1994). The underlying assumption that a larger proportion of dry matter produced under CO_2 enrichment is preferentially allocated to roots and increased under limiting water and nutrient supply needs to be evaluated. Differences among experiments can be attributed to crop type, genotypes, resource supply (water and nutrients), and other experimental factors, that is, duration and method of exposure, and interacting treatment variables (Idso et al., 1988; Rogers et al., 1996). This is further complicated by poor estimate of C returned to the soil via the death of fine roots at harvest leading to an underestimation of C allocation (Stulen and den Hertog, 1993). Recent observations of in situ root dynamics from nondestructive monitoring methods reveals estimates of net belowground production significantly underestimates gross production (Fahey and Hughes, 1994; Hendrick and Pregitzer, 1992, 1993a, 1993b). Berntson and Bazzaz (1997a) argued that elevated CO_2 increases the magnitude of cumulative gross production and cumulative gross root loss with a large seasonally dependence on these responses. Elevated CO_2 enhances gross production of roots early in the growing season, before maximum root length and enhance cumulative gross loss of roots in the latter portion of the growing season after maximum root length had been achieved. They concluded that static assessments of belowground productivity may underestimate gross fine root productivity and turnover, and this bias may be exaggerated with elevated CO_2. Stulen and den Hertog (1993) list several reasons why determination of R/S is subject to experimental error; including problems in defining the R/S boundary, quantitative recovery of roots (especially fine roots), root decomposition, nutrient and water regime in the soil, ontogenetic effects, and accumulation of non-structural carbohydrates.

Root Length and Rooting Depth

When exposed to increased CO_2, roots have been observed to become more numerous, longer, thicker, and faster growing in crops (Chaudhuri et al., 1990; Prior et al., 1994a, 1994b, 1995) with increased root length in many plant species (Norby, 1994; Rogers et al., 1999; Pritchard and Rogers, 2000; Bernacchi et al., 2000). Root distributions with depth of sorghum with elevated CO_2 was studied by Pritchard et al. (2006) and they concluded the greatest root length was observed between 4- and 15-cm soil depths. At physiological maturity, a larger percentage of total root length had died at shallow soil depths compared to deeper depths; for example, 87% of roots produced at the shallow soil depths died before harvest compared to 48% at the lower depths. Daily production of new roots occurred primarily in the early part of the growing season and the maximum root length production per day occurred when mortality and production rates were nearly equivalent at approximately 59 d after planting.

Lengths and volumes of taproots, lateral roots and fine roots were higher for CO_2–enriched cotton plants (Prior, 1992; Prior et al., 1994a, 1994b; Rogers et al., 1993). A 110% increase in root length of soybean was observed as CO_2 concentration increased from 350 to 700 μmol mol^{-1} (Rogers et al., 1992). Increased root length and number was found in sweet potato (Bhattacharya et al., 1990), and in *P. acutifolius* and *P. vulgaris* (Salsman et al., 1999). Increased stele and cortex diameter, root diameter in the root hair zone, length of unbranched first order lateral roots, total root length, and root volume was increased in cotton with increased CO_2 (Rogers et al., 1992).

Temperature and CO_2 effects were studied in groundnut and total root length increased with increasing CO_2 from 400 to 800 μmol mol^{-1} at both low and high temperatures (Pilumwong et al., 2007). Although the difference was not significant, there was an observed increase of 13% when plants were grown at 600 μmol mol^{-1} CO_2, and 20% at 800 μmol mol^{-1} CO_2. However, visible root length, root number, and root length density increased with CO_2 increases from 400 to 800 μmol mol^{-1} at 25/15°C, but decreased as CO_2 increased when temperatures increased to 35/25°C (maximum/minimum temperature). Root branching was the primary factor affecting total length and volume of roots. Berntson and Woodward (1992) concluded CO_2 enrichment resulted in more branched and longer root system of *Senecio vulgaris*. Many studies have found elevated CO_2 resulted in more and/or longer plant roots or faster root growth, possibly leading to increased penetration of the soil profile (Baker et al., 1990; Chaudhuri et al., 1990; Rogers et al., 1992) and/or horizontal spread of the roots (Idso and Kimball, 1991)

Root length and number have been the most frequently evaluated in horticultural species (45 and 74% of studies, respectively) compared with plants in other categories (2–12%). A majority (61–100%) of studies found that increased CO_2 resulted in more and/or longer plant roots (Rogers et al., 1994) which led to increased depth (Baker et al., 1990; Rogers et al., 1992) and/or horizontal spread (Idso and Kimball, 1991, 1992) (Table 1).

Rooting depth has important implications for hydrology, biogeochemistry, and primary productivity of terrestrial

ecosystems (Jackson et al., 1997) and since the depth of plant roots depends on a variety of conditions, including soil properties, vegetation type, nutrient availability, and climate there are a number of potential implications from rooting depth response to CO_2 (Guswa, 2010). A number of papers and reviews describe the genetic control of root architecture and the variation between plant types and individual plant cultivars about the maximum rooting depth (Kell, 2011). Plant root depths vary greatly in similar soils for different organisms (e.g., Burch and Johns, 1978; Jackson et al., 1996; Jobbagy and Jackson, 2000), and varies substantially within the same soils or growth media for different cultivars of the same plant, and between different cultivars of the same parent.

Canadell et al. (1996a) reviewed rooting depth from 290 observations of maximum rooting depth for 253 woody and herbaceous species and found maximum rooting depth ranged from 0.3 m for some tundra species to 68 m for *Boscia albitrunca* in the central Kalahari. In this analysis, 194 species had roots at least 2-m deep, 50 species had roots with a depth of 5 m or more and 22 species with rooting depth to 10 m or deeper (Canadell et al., 1996a). The average rooting depth from this comparison was 4.6 ± 0.5 m. When the maximum rooting depth was segregated by biome the results showed 2.0 ± 0.3 m for boreal forest, 2.1 ± 0.2 m for cropland, 9.5 ± 2.4 m for desert, 5.2 ± 0.8 m for sclerophyllous shrub land and forest, 3.9 ± 0.4 m for temperate coniferous forest, 2.9 ± 0.2 m for temperate deciduous forest, 2.6 ± 0.2 m for temperate grassland, 3.7 ± 0.5 m for tropical deciduous forest, 7.3 ± 2.8 m for tropical evergreen forest, 15.0 ± 5.4 m for tropical grassland/savanna, and 0.5 ± 0.1 m for tundra. If the aggregation was conducted across species within biomes (except croplands) by three basic functional groups maximum rooting depth was 7.0 ± 1.2 m for trees, 5.1 ± 0.8 m for shrubs, and 2.6 ± 0.1 m for herbaceous plants. These analyses data show that deep root habits are quite common in woody and herbaceous species across terrestrial biomes, deeper than previously assumed. These results argue for an enhanced understanding of ecosystem function and its application in developing ecosystem models.

Carbon dioxide enrichment resulted in enhanced root proliferation at shallower soil depths in wheat (Chaudhuri et al., 1990; Fitter et al., 1996; Van Vuuren et al., 1997; Van Vuuren et al., 1997), cotton (Rogers et al., 1992), sorghum (Chaudhuri et al., 1986), and grassland (Fitter et al., 1997). Chaudhuri et al. (1990) found winter wheat grown under elevated CO_2 achieved maximum rooting penetration significantly faster than plants grown in ambient air. They also found that root growth differences between ambient and elevated CO_2 occurred in the upper 10 cm of soil and concluded that high levels of CO_2 compensate for restriction in growth of wheat roots by drought. In contrast to wheat, Chaudhuri et al. (1986) found root numbers and dry weights of sorghum roots were higher at all depths to 150 cm under increased CO_2. Controlled studies on rooting pattern of cotton plants under FACE (Prior, 1992; Prior et al., 1994a, 2003; Rogers et al., 1993) demonstrated that root architecture, defined as the distribution of fine root density per unit volume of soil and expressed as length or dry weight per m^3, increased both vertically and horizontally with increased CO_2. Fine root density increased under CO_2 enrichment to 90 cm with the most significant increase in the upper 45 cm. Root length and dry weight densities exhibited greater difference between ambient and elevated CO_2 as distance from row center increased, indicating faster and more prolific spread of cotton roots (Rogers et al., 1994).

Experimental evidence from forested ecosystems shows CO_2 enrichment may lead to deeper rooting distributions (Rogers et al., 1994). Altered rooting distributions will affect ecosystem processes and the depth to which fine roots are produced influences root chemistry, physiological function, and mycorrhizal infection, leading to altered N uptake rates and slower root turnover. Changes in rooting patterns influence nutrient dynamics, thus influencing crop performance when nutrient demand is high. Whole plant nutrient uptake is often higher, while tissue nutrient concentration is reduced for CO_2–enriched plants (Prior et al., 1998, 2003; Rogers et al., 1994, 1997). Shifts in rooting patterns alter their competitive effectiveness for edaphic resources. Root proliferation into nutrient-rich zones can be an important mechanism in the exploitation of soil resources (Borkert and Barber, 1985; Jackson and Caldwell, 1989).

Root Branching

The branching patterns of root systems have been described as "developmentally" (Barley, 1970; Rose, 1983) and "topologically" (Fitter, 1985, 1986, 1987). Previous studies show the primary response of crop plants to elevated CO_2 on branching and extension of first-order and higher-order laterals root over the extension of the root system deeper into the soil (Rogers et al., 1999; Pritchard and Rogers, 2000). They suggested that, with higher atmospheric CO_2 concentrations, crop roots will be larger, more highly branched (especially at shallow depths), but less efficient in nutrient and water uptake (decreased specific root activity). This hypothesis is supported from observations by Berntson and Bazzaz (1995), demonstrating the potential of root systems to acquire resources may increase because of greater total root length densities; however, there may be a decline in the efficiency of resource capture. Root systems of crops grown in CO_2–enriched environments are often more branched, especially at shallower soil depths, compared to roots of crops grown in ambient air (sorghum, Chaudhuri et al., 1986; wheat, Chaudhuri et al., 1990; Fitter et al., 1996; *Caratonia siliqua*, Cruz et al., 1997; soybean, Del Castillo et al., 1989; cotton, Rogers et al., 1992; Pilumwong et al., 2007; *Senecio vulgaris*, Berntson and Woodward, 1992). These observations indicate altered belowground plant function suggesting higher level soil ecological processes may change as atmospheric CO_2 continue to increase (Pritchard and Rogers, 2000; Rogers et al., 1997, 1999).

In soybean, Del Castillo et al. (1989) reported no effect on rates of elongation; however, there was an increase in the number of more highly branched roots. Cruz et al. (1997) reported that carob (*Ceratonia siliqua* L.) seedlings grown in elevated CO_2 produced more lateral roots and shorter and thicker roots. In a FACE study with cotton, Rogers et al. (1992) showed that the number, length, and mass of lateral roots were enhanced by CO_2 enrichment. Although taproot diameter, mass, and volume were enhanced, length was not affected. In contrast, Rogers et al. (1992) reported an increase in soybean root length but no change in the number of lateral roots. Under FACE studies, the lengths and volumes of taproots, lateral roots, and fine roots were higher

for CO_2–enriched cotton plants but the number of lateral roots per unit length of taproot was not significantly increased, the greater taproot lengths with CO_2 enrichment increased total number of laterals (Prior, 1992; Prior et al., 1994a, 1994b; Rogers et al., 1993). Another FACE study on spring wheat by Wechsung et al. (1999) reported a 37% increase in total root dry mass in the FACE vs. control plots during stem elongation. During early vegetative growth, root dry mass from the inter-row space was significantly higher for FACE compared to control treatments suggesting that elevated CO_2 promoted the production of first-order lateral roots per main axis. During the reproductive period of growth, more branching of lateral roots was found in the FACE treatment along with significantly higher root dry mass when soil water supply was limiting. These responses in root growth and morphology to elevated CO_2 and reduced soil water supports the hypothesis that plants grown in a high CO_2 environment may compensate for soil water stress because of the increased root density ability to extract more water per unit soil volume.

Differential effects of CO_2 concentration on root branching may lead to altered root architecture and ability of roots to extract water and nutrients. For example, Berntson and Woodward (1992) observed for *Senecio vulgaris* grown under elevated CO_2 more horizontal branching angles of roots leading to greater horizontal root spread. Rogers et al. (1992) observed longer second-order laterals in soybean, which could lead to deeper root penetration and greater exploration of soil for nutrients and water but could ultimately lead to competition among roots in resource-limited environments. Conversely, Del Castillo et al. (1989) found more roots attributed to increased branching rather than longer roots in soybean grown under enriched CO_2. The positive effect of increased root numbers leads to more efficient exploration of the same volume of soil compared to deeper root penetration (Pritchard et al., 1999). Increasing CO_2 caused increased root branching across species suggesting that greater root exploration of the profile would occur as a result of the positive effect of CO_2 on root growth (Table 1).

Root Thickness, Quality, and Diameter

The additional root biomass production from elevated CO_2 induced increased thickness or diameter or quality (root length density) of plant roots and increased total root length and volume along with root diameter in the root hair zone and length of unbranched first-order laterals (Rogers et al., 1992). Roots become more numerous, longer, thicker, and faster growing in crops grown under high CO_2 (Chaudhuri et al., 1990; Prior et al., 1994a, 1994b, 1995) and the diameters of dead roots did not differ from the diameter of roots that remained alive during the crop growth period of sorghum (Pritchard et al., 2006). Changes in root dry weight density caused by CO_2 enrichment suggests possible changes in root quality. The results of a FACE experiment on cotton by Prior et al. (1994a, 1994b) showed large shifts in root dry weight density. These results suggest possible changes in root quality from changes in root dry weight density through changes in tissue density of roots (fine and taproots) resulting in shifts in carbohydrate storage, cell number, cell size, and percentage of intercellular space or other structural modifications. Soybean plants grown under CO_2 enrichment exhibited a 27% increase in root diameter, stele diameter (23%), and cortex width (28%) in the root hair zone (Rogers et al., 1992). Studies on structural aspects of plant roots (i.e., diameter, volume, branching, relative growth rate, etc.) have usually shown positive effects of high CO_2. Tubers (number, dry weight, diameter, etc.) and nodulation (number, dry weight, activity, etc.) benefit from elevated CO_2 in most crops (Rogers et al., 1994).

Zhao et al. (2000) germinated pea (*Pisum sativum* L.) seeds and exposed the young plants to various atmospheric CO_2 concentrations in controlled environment chambers to determine if elevated CO_2 impacted root border cells, which are major contributors of root exudates in most agronomic plants. They found elevated CO_2 increased the production of root border cells in pea seedlings. Changing the ambient air to air enriched with 3000 and 6000 μmol mol^{-1} CO_2, border-cell numbers increased by more than 50 and 100%, respectively. It is likely that continued increases of CO_2 will likely produce greater numbers of root border cells in crop plants and lead to increased amounts of root exudates into the rhizosphere, suggesting that associated soil microbial and fungal activities would be stimulated from increases in plant-derived C inputs. These changes should make the soil environment more favorable for plant growth and development in a high CO_2 environment. Few studies have addressed CO_2–induced changes in root quality/thickness/diameter and structure and further research is needed, especially under field environments (Table 1).

Root Mortality/Root Turnover

Root turnover is important to the global C budget as well as to nutrient cycling in ecosystems and to the success of individual plants in obtaining water and nutrients. Replacement of older roots with newly formed roots is referred to as root turnover. Root turnover is estimated from the difference between cumulative births and deaths, which represents either a net accumulation or disappearance of roots. If roots are not accumulating even though production is enhanced, then turnover must be equally enhanced (i.e., birth rate equals death rate). The difference in accumulation rate between elevated and ambient CO_2 levels can be used to determine whether turnover is affected by CO_2 and a positive difference means that roots are accumulating faster under elevated CO_2. There are several papers discussing approaches for estimating annual root turnover (Milchunas et al., 1985; Caldwell and Eissenstat, 1987; Hendrick and Pregitzer, 1992; Milchunas and Lauenroth, 1992; Hendricks et al., 1993; Fahey and Hughes, 1994), which reveal no consensus on the best approach for estimating root turnover. Del Castillo et al. (1989) observed a significant linear increase in the number of actively growing roots of soybean with increased CO_2 compared to elongation rate. Eissenstat et al. (2000) applied an efficiency model to hypothesize that rising CO_2 would increase average root lifespan. In contrast, other investigators have suggested root lifespan is unlikely to change with increasing CO_2 (Pritchard and Rogers, 2000; van Noordwijk et al., 1998).

Increased photosynthesis under elevated CO_2 stimulates belowground C input, fine-root growth (Curtis, 1996; Curtis and Wang, 1998; Pendall et al., 2005) and root turnover rates and biomass (Berntson and Bazzaz, 1997b; Fitter et al., 1999; Allen et al., 2000; Pregitzer et al., 2000; Wan et al., 2004). Increased fine-root production and mortality are associated with higher temperatures (Gill and Jackson, 2000) and turnover rates (Hendrick and Pregitzer, 1993b, 1997; Forbes et al.,

1997; Fitter et al., 1999; King et al., 1999; Wan et al., 2004). Turnover rates increase with increased C allocation to root systems when plants are grown under elevated CO_2, at least in grasslands and forest (Fitter et al., 1996). Root life span is highly variable, from a few weeks in some plants to a few years in others (Eissenstat and Yanai, 1997). Root longevity varies widely within an individual species.

Fine roots are essential for plant water and nutrient uptake, soil C input, and soil microbial activity (Eissenstat, 1992; Norby, 1994). Turnover of fine roots (<2.0-mm diam.) play a critical role in regulating ecosystem C balance and accurate estimates of belowground net primary productivity (NPP) are required for estimating net ecosystem productivity (NEP) (Pendall et al., 2005). As much as 33% of global annual NPP has been estimated for the production of fine roots (Jackson et al., 1997). Caldwell (1977) suggested for perennial systems, at least 25% of root systems die and replaced annually, accounting for as much as 50 to 80% of net production. Death of older roots and the growth of new ones are a significant energetic cost to the plant (Canadell et al., 1996b). Understanding the trade-offs between the cost of maintaining old roots compared with that of growing new ones is an important step in understanding how increased C assimilation, associated with rising global CO_2 affects root turnover. van Noordwijk et al. (1998) developed a quantitative model for this system by estimating for a root with a growth respiration of 2 g CH_2O g^{-1} root dry weight and a maintenance respiration of 0.03 g Cg^{-1} root dry weight, approximately 60 d of root maintenance in unfavorable conditions would cost as much as one cycle of root death followed by regrowth. van der Werf et al. (1988) showed, for a different species, that the adenosine-5'-triphosphate (ATP) costs of producing 1 g fresh wt. of root is approximately equal to the cost of maintaining 1 g of root for 10 d. The implications of this energy balance for roots suggest it may be more energetically expensive to maintain one root when the costs of maintenance during periods of stress exceed the energy requirements of growing new roots on the return of favorable soil conditions.

The availability of underground resources (water and nutrients) influences the C allocation to roots and turnover rates. If we follow the argument of Stulen and den Hertog (1993) that plants grown under non-limiting conditions do not alter their allocation of C between roots and shoots under elevated atmospheric CO_2 then the hypothesis of van Noordwijk et al. (1998) that increasing atmospheric CO_2 is not likely to have a significant direct effect caused by a greater C supply on root turnover. However, indirect effects, mediated by shifts in plant water availability and nutrient relations, are likely to affect root turnover. Experimental evidence shows that root turnover increases more often than not when soil conditions are limiting root uptake (Pregitzer et al., 1995; Canadell et al., 1996b). Canadell et al. (1996b) found from four experiments with grass systems there was increased root turnover in three with no change in one experiment. In four experiments on trees, increased turnover was observed in three, while one showed a decrease (Canadell et al., 1996b). Finally, no difference in root turnover was observed in wheat grown in elevated CO_2 (Fitter et al., 1996). It is likely that root turnover will be different between annual and perennial plants.

Temporal pattern of root growth is consistent with C allocation to roots being highest during early vegetative growth and decreasing as plants mature and transition to reproductive growth (Swinnen et al., 1994). Pritchard et al. (2006) concluded daily production of new roots in sorghum occurred primarily in the early part of the growing season and daily mortality of roots increased steadily over the growing season in a linear fashion under elevated CO_2. The death of roots and growth of new roots corresponds to the availability of soil water and nutrients (Huck et al., 1987; Smucker, 1993). Huck et al. (1987) found that birth and death rates of roots were mediated in time by rainfall events and in space by moist soil microsites. They observed that the number of active soybean roots decreased after each rain, increased rapidly during dry periods, and declined after subsequent rainfall events. They observed spatial peaks in root growth during dry conditions occurred in the soil profile where soil moisture was favorable (Huck et al., 1987). Resource availability (nutrients, moisture, and temperature) in the top layer of soil plays a key role on the rate of fine root mortality. Pritchard et al. (1999) found a negative linear relationship between soil depth and the proportion of roots that died in sorghum with a similar conclusion made on alfalfa roots (Goins and Russelle, 1996; Watson et al., 2000), groundnut (Krauss and Deacon, 1994), and sugar beet (van Noordwijk et al., 1994). Changes in nutrient availability, temperature, and moisture throughout a day with depth a possible explanation for these observations because of the greater change in the upper soil layers compared to deeper layers (Watson et al., 2000). In tree species, rates of fine root mortality was roughly twice as in trees grown at elevated CO_2 compared to ambient CO_2 in both high and low soil N (Pregitzer et al., 1995).

The projected increases in air temperatures, changing precipitation patterns, and potential decreases in soil nutrients availability could be expected to have impacts on root mortality (Rastetter et al., 1997). Root mortality might be accelerated by decreases in soil moisture (Klepper et al., 1973; Hayes and Seastedt, 1987; Huck et al., 1987) or by increases in soil temperature (Fitter et al., 1999). However, root mortality might be reduced by decreased availability of nutrients (Eissenstat and Yanai, 1997). Fitter et al. (1997) observed in peat and limestone grassland soils, cumulative root birth and death totals were greater under elevated CO_2. In the peat soil, cumulative births were 20% greater (36 as compared to 30 per tube) and deaths 21% greater (34 and 28 per tube) after two seasons under elevated CO_2. In the limestone soil, cumulative births were increased by 30% (35 vs. 27) and deaths by 29% (31 vs. 24). Turnover was faster under elevated CO_2 in the peat soil, but there was only a small effect on turnover in the limestone soil (Fitter et al., 1997).

Finally, it's suggested that more long-term studies are needed, to detect both existing patterns of root mortality and lifespan with resource availability and plant strategy, and to progress beyond short-term studies, which may be misleading. Factors that should be included in studies of root lifespan, in addition to resource availability, include root age, plant C status, and pathogen pressure. The effects of increasing CO_2 on root mortality are less clear and the linkage to changes in temperature and soil water has been difficult to quantify.

Conclusions and Recommendations

Crops grown under elevated atmospheric CO_2 exhibit changes in above- and belowground growth responses which

could potentially lead to alteration in plant communities. Increased allocation of C to roots may stimulate lateral rooting with extensive root branching. Rooting depth of roots will be influenced by availability of water, nutrients, and other resources in the soil profile. The greater proliferation of roots under elevated atmospheric CO_2 will lead to higher extraction of soil resources with less efficient rooting systems. Carbon dioxide often suppresses plant water use, increasing water use efficiency with relatively less water flow within the plant and consequently in the soil matrix. The enhanced proliferation of roots grown under elevated atmospheric CO_2 concentration may be a strategy which permits adequate nutrient acquisition in the absence of normal water absorption rates. Deeper roots could penetrate into deeper soils to create more resilience to droughts in natural plant communities and agronomic crops. This deeper rooting would be an advantage if climates became drier and altered belowground plant competition.

Variability in response of plant root to CO_2 have been observed in response to the interacting effects of CO_2 with other climatic factors and soil resources coupled with species and even genotypic variability along with levels of the treatment variables. In addition, environmental changes concomitant with the rise of atmospheric CO_2 levels might substantially modify plant and ecosystem level responses. For example, some studies suggest that plants subjected to water stress will respond more favorably to elevated CO_2 while other studies report the opposite response.

Enhanced root growth and biomass production from exposure to increased CO_2 concentrations could deliver more C to the soil profile potentially altering rhizosphere microbiology (populations and dynamics); and inducing possible physicochemical changes in soil by increasing root activity, including rhizodeposition due to root turnover. It is evident from several studies that increasing levels of CO_2, will have virtually no adverse effects on plant root growth except where decreases in efficiency of root systems (specific root activity) and inability of roots to acquire nutrients due to reduced water use/uptake to keep pace with the increased C assimilation would have negative consequences on crop productivity and nutrient content in aboveground organs.

Under favorable conditions of water and nutrients for growth, dry matter partitioning to the root is not altered by CO_2 enrichment. The increase in R/S, frequently observed under limiting conditions of water and/or nutrients, enables the plant to explore a greater soil volume and extract more water and nutrients. However, there are many debates on whether R/S is valuable as a standard root variable due to our inability to accurately estimate belowground biomass, particularly fine roots, root turnover biomass at later stages of the crop and at deeper soil depth apart from microbial decomposition of roots. As observed from many studies, plants allocate more C toward the root growth in the early vegetative stage of development and then decrease. Static assessments of belowground productivity at different stages of crop growth may greatly underestimate the root biomass leading to an exaggeration of R/S values.

Root lifespan has important consequences for plant growth and productivity, plant competition, and C and nutrient cycling. Very limited information is available to quantify the effects of elevated CO_2 on the trade-offs associated with maintaining old roots in comparison with growing new roots. Long-term studies are needed to detect existing patterns of root lifespan with resource availability and plant strategy and to progress beyond short-term responses to treatments. Factors that should be included in studies of root lifespan in addition to resource availability include root age, plant C status, and pathogen pressure. Because root lifespan differs from leaf lifespan in many species, better knowledge of root lifespan may result in revision of current theories regarding plant adaptation and growth strategies.

Agricultural management practices may have a greater impact on root growth than rising atmospheric CO_2 since management practices influence soil physical, chemical, and biological properties of soil, and consequently root growth dynamics. Less understood are the interactive effects of elevated CO_2 and management practices (tillage, soil moisture, and nutrients) including drought on root dynamics, fine-root production and water-nutrient use efficiency, and the contribution of these processes to plant growth in water and nutrient-limited environments. Increases in water use efficiency and reductions in water use can contribute to enhanced soil water content under elevated CO_2.

Roots are difficult to study because they are hidden within the soil profile and extraction methods destroy the sample. The advent of nondestructive techniques, that is, minirhizotrons or rhizotrons, provide a method of visual and qualitative assessments but do not permit quantitative evaluations of the changes in root biomass or detailed examinations of the branching or root turnover rates. The current state of knowledge regarding root systems is rather simplistic because of the methodological limitations; however, these studies have begun to show that there will be effects of increasing CO_2 on the roots along with the shoots and these responses will have impacts on the utilization of the soil resources, water, nutrients, gases, and temperature. We can continue to strive for more detailed understanding of root responses to changing CO_2; however, these should not be done without considering the interactions with the soil environment. An aspect which is evident from the combined literature is that root function under increased CO_2 does increase when there is no limitation from water, nutrients, or temperature which does suggest that under climate change adoption of management practices which reduces the occurrence of these stresses will have a positive benefit on plant growth and productivity. Understanding these processes will provide the foundation for design of future adaptation and mitigation strategies linking improved soil management practices with crop and root response to increasing CO_2 and will provide a structure for improving the stability of agriculture under climate change.

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